Modelling the effect of temperature on the maximum growth rates of phytoplankton populations

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Abstract

Functional relationships which parameterize growth based on the Eppley temperature relationship for phytoplankton maximal growth rates are increasingly being used in marine and freshwater ecosystem models. In this paper, we demonstrate the effect of using such generalized relationships in modelling studies. Two suites of numerical experiments are carried out to investigate the sensitivity of models to generalized growth relationships. In each experiment, 100 individual species or groups of phytoplankton are allowed to compete under a variety of growth versus temperature relationships. One suite of experiments is carried out within a simple 'chemostat' type model that is forced with seasonally varying temperature and photosynthetically available radiation (PAR) fields. A second suite of experiments is carried out using a biogeochemical mixed-layer model to demonstrate the sensitivity of these models to various temperature versus growth relationships. The key difference in the biogeochemical mixed-layer simulations is in the timing of the ecosystem response to seasonal variability of the mixed-layer depth and temperature. The Eppley growth versus temperature relationship overestimates phytoplankton growth by as much as 80% during the spring when growth rates are crucial to the timing of the spring blooms. This decrease in growth rates causes a delay in the spring phytoplankton bloom which in turn results in significant changes in all other model constituents. The results from both suites of experiments show that it is important to resolve the intrinsic growth dynamics of a population in order to properly resolve the maximum growth rates of phytoplankton populations. The results also present a possible explanation for why phytoplankton are commonly found growing within water colder than their optimal temperature for growth. A dynamic growth versus temperature model is introduced that is capable of resolving the growth dynamics of a population of phytoplankton under a variety of temperature forcing scenarios. This new growth versus temperature model/relationship will be useful in global biogeochemical models and demonstrates the importance of underlying population dynamics in controlling bulk community growth estimates.
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1. Introduction

General circulation models (GCM) are currently being coupled to ecosystem models in order to simulate global ocean ecosystems. These circulation models are based on well-understood equations of motion, state, and continuity. Marine ecologists have yet to discern such relationships or 'laws'. The development of ecological theory with applicable equations for use in models has been slow, and the testing of these theories has been difficult due to the complex interactions between organisms and their environment.

Historically, modelling the ocean's ecosystem has been approached from an empirical perspective. Typically, ecosystem modelers develop or assemble a set of empirically-derived functions for

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each of the specific trophic levels and use these to control the flow of material between the model's components. These functions are then a fixed set of equations that are not allowed to acclimate to changes in the ecosystem that may arise naturally, such as changes in nutrient flux, temperature, light, species succession, competition, food availability, predation, and phenotypic, or on longer time scales, genotypic, changes. There are currently no ecosystem models that are based entirely on first principles (Behrenfeld and Falkowski, 1997a; Evans and Fasham, 1993). Models are generally based upon some level of empirical or bulk parameterizations. The task is to decide upon what level to parameterize the individual processes in order to accurately quantify the observed system response.

Microalgae are capable of carrying out photosynthesis and cellular division over a wide range of temperatures. The effects of temperature on marine algae have been studied extensively for many years (Berry and Bjorkman, 1980; Berry and Raison, 1981; Davison, 1991). It is well-known that phytoplankton have an optimal temperature for growth (Li, 1980). Below the optimal temperature, plant growth rates increase with temperature according to their individual Q_{10} value. The Q_{10} relationship is often parameterized using the Arrhenius function, but in a physical chemistry framework, its shape is controlled by the net effect of the Maxwell–Boltzmann relationships from all of the cellular processes which are linked to Calvin cycle enzymatic activities (Falkowski, 1980). Above the optimal temperature, growth rates decrease due to inactivation or denaturation of proteins or other factors (Ratkowsky et al., 1983).

While a general shape occurs for each growth versus temperature curve, the individual shapes vary widely between different species, and even clones of the same species (Jorgensen, 1968; Falkowski, 1977; Smayda, 1969; Yoder, 1979; Suzuki and Takahashi, 1995). The reasons for this wide range in variability may not be caused solely by temperature variability but also by changes in nutrient and light conditions under which they were grown. The optimal temperature for the curves also varies with changes in the temperature at which the phytoplankton are grown (Li, 1980). However, despite differences in the shapes of the temperature versus growth curves, a general equa-

tion can be derived for maximal growth. Eppley (1972) assembled a limited data set of growth curves from phytoplankton batch cultures. From this data set, an empirical equation was derived for estimating the maximum growth rate based on temperature, $\mu_{max} = \log(2)\,0.851(1.066^{T})$, for a given temperature, T. Other growth rate versus temperature relationships have been proposed using data from other laboratory experiments (Ahlgren, 1987).

5. Conclusions

Our results demonstrate the importance of intrinsic population variability on ecosystems. The model results show that phytoplankton population growth rates do not resemble the Eppley (1972) relationship that, to date, all global ecosystem models use, nor many of the other relationships presented in Behrenfeld and Falkowski (1997a), Falkowski et al. (1998). However, the resulting population growth curves (c.f. Fig. 6) are very similar in shape to the growth versus temperature relationship obtained by Behrenfeld and Falkowski (1997b), Balch and Byrne (1994). The major differences in these curves is that the resulting growth relationship presented in this paper does not account for nutrient- and light-limitation. It is hoped that the results from this study will help lead to the development of better primary production models.

A new model for determining the maximum growth rate for a population of phytoplankton is presented that takes into account the general shape of the individual phytoplankton growth versus temperature relationships and the variability of the temperature. This new model is unique in that it is capable of resolving species succession within the global ecosystem and retains the intrinsic variability or dynamics of the population as a whole. At present, this new formulation has yet to be tested within a GCM framework. The results from the new formulation are robust when compared against simulations with 100 plus phytoplankton. Further efforts will focus on the effects of nutrient uptake variability with the hope of establishing a similar global model.

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